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Variation in growth, wood density and carbon concentration in five tree and shrub species in Niger

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Abstract There is little information about variation in growth, wood density and carbon concentration in native tree and shrub species in Africa. This information is needed to make realistic projections about carbon sequestration of different species in different environments. Farmers manage natural regeneration of many native species in the drylands of Niger, so there is interest in carbon sequestration potential of the species. The objectives of this study were to determine: (1) if tree height, stem diameter, mean ring width, wood density and carbon concentration differ among five tree and shrub species (*Combretum glutinosum*, *Combretum micranthum*, *Combretum nigricans*, *Guiera senegalensis*, *Piliostigma reticulatum*) in Niger; (2) if variation within species is affected by land use type (parkland agroforests, woodlands), soil type (sandy, rocky), terrain type (temporarily flooded, flat, hill slope) and mean annual rainfall; and (3) if growth variables, wood density and carbon concentration are correlated in the five species. Environmental variables did not have strong effects on growth and wood variables of the species, and some effects differed among species. Height across species increased with mean annual rainfall. Stem diameter and mean ring width across species were greater in parkland agroforests than in woodlands. Carbon concentration was positively correlated with growth variables of four species, but was not correlated with wood density in most species. Correlations between wood density and growth differed in sign among some species. We conclude that above-ground carbon sequestration per tree probably increases with mean annual rainfall and is greater in parkland agroforests than in woodlands.

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Introduction

Farmers select and protect natural regeneration of many native tree and shrub species in the drylands of Niger and neighboring countries in West Africa (Haglund et al. 2011). This practice, known as 'farmer managed natural regeneration' (FMNR), has been widely adopted because it is simple and inexpensive, contributes significantly to rural livelihoods, can restore woody vegetation in degraded landscapes and conserve biodiversity. FMNR is practiced mainly in parkland agroforests, which are managed for the production of food crops, trees, shrubs and domestic livestock (Boffa 1999), but also in forests located near villages. Farmers manage and conserve more than 50 native tree and shrub species in these land use systems in Niger because they provide essential products (mainly wood, food, fodder and medicines) and environmental services (soil-fertility improvement, soil/water conservation, shade) (Faye et al. 2011). Because farmers want to maintain these species in parkland agroforests and forests, there is interest in the carbon sequestration potential of the species to help mitigate anthropogenic climate change (Luedeling and Neufeldt 2012).

Carbon content in a tree stem depends on wood density, carbon concentration and wood volume, which is a function of tree height and stem diameter (Castaño-Santamaria and Bravo 2012). Information about variation in tree height, stem diameter, wood density and carbon concentration among and within species is needed in order to make realistic projections about carbon sequestration of different species in different environments. This information is limited in Africa, which contains the largest land area in the tropics. For example, the effect of rainfall on tree growth has been studied in only about 15 species in Ethiopia, Mali and Zambia (Chidumayo 2005; Gebrekirstos et al. 2008; Sotelo Montes et al. 2014). Mean values for wood density and carbon concentration have been published for about 35 species in humid tropical forests of Ghana and Uganda (Becker et al. 2012; Yeboah et al. 2014). Mean values for wood density have also been published for about 45 species in dry tropical forests of Burkina Faso and Mali (Nygård and Elving 2000; Sotelo Montes et al. 2012), but there are no published data on carbon concentration of species in Africa's dry tropical forests. Intra-specific variation in wood density has been studied in only five species in dry tropical forests in Mali (Sotelo Montes et al. 2012, 2014), and intra-specific variation in carbon concentration has not been studied in any species in Africa.

Based on previous research, one might expect the following geographical trends in tree growth and wood density, and correlations between growth, wood density and carbon concentration. (1) Tree height and stem diameter may be greater in locations with higher mean annual rainfall (Chidumayo 2005; Gebrekirstos et al. 2008). However, the effect of rainfall on growth may not be significant if the species produces deep roots and can extract soil water during the dry season (Gourlay 1995), and the effect may be negative if the species grows slowly and is shaded by faster-growing species in locations with higher rainfall (Sotelo Montes et al. 2014). (2) Wood density may be greater in drier locations. Trees in drier locations, especially taller trees, may produce narrower vessel lumen and thicker vessel walls (i.e., denser wood) compared with trees in more humid locations in order to protect against vessel implosion and cavitation (Lachenbruch and McCulloh 2014). Taller trees may also require denser wood at the base of the stem to increase the stem's mechanical strength and stiffness and, thereby, resist bending stresses produced by wind (Lachenbruch and McCulloh 2014). (3) Wood density may be positively correlated with carbon concentration (Elias and Potvin 2003; Thomas and Malczewski 2007; Becker et al. 2012). Vessel walls are composed of cellulose and lignin (Martin and Thomas 2011), so thicker walls have a higher carbon concentration than narrower walls. This could result in a positive correlation between wood density and carbon concentration (Lachenbruch and McCulloh 2014). (4) Tree height may be positively correlated with wood density (Sotelo Montes and Weber 2009; Weber and Sotelo Montes 2010; Sotelo Montes et al. 2014). This correlation may primarily reflect the hydraulic function of denser wood in drier locations, but the mechanical function of denser wood in more humid locations (Williamson and Wiemann 2010). (5) Tree height may also be positively correlated with carbon concentration. This follows from the third and fourth points above.

We selected five species for this study in Niger: *Combretum glutinosum* Perr., *Combretum micranthum* G. Don., *Combretum nigricans* Lepr. ex Guill. and Perr., *Guiera senegalensis* J. F. Gmel. and *Piliostigma reticulatum* (DC.) Hochst. Variation in growth and wood density of *C. glutinosum*, *G. senegalensis*, *P. reticulatum* and two other species was studied in Mali: results indicated that growth and wood basic density differed significantly among some species; growth (but not wood basic density) of some species differed significantly among land use, soil and terrain types; mean annual rainfall did not have a significant positive effect on growth and wood basic density in any species; and growth and wood basic density were positively correlated in only one species (Sotelo Montes et al. 2012, 2014, 2017a).

This study has three objectives: (1) determine if growth variables (height, stem diameter, mean ring width), wood basic density and carbon concentration differ among the five species in Niger; (2) determine if variation within species is affected by land use type (parkland agroforests, woodlands), soil type (sandy, rocky), terrain type (temporarily flooded, flat, hill slope) and mean annual rainfall; and (3) determine if growth variables, wood basic density and carbon concentration are correlated in the five species.

Materials and methods

Study region, species studied, tree sampling and site variables

The study was conducted in the Sahelian and Sudanian ecozones of southern Niger. The Sahel is a semi-arid ecozone between the more humid Sudanian ecozone to the south and the Sahara Desert to the north, so there are steep rainfall gradients with latitude and also with longitude (Buontempo 2010: lower rainfall in north and east). The rainy season lasts 3–4 months per year (ends generally in September), and is followed by a long, hot dry season. Mean annual temperature is 29 °C, and afternoon temperatures often exceed 45 °C at the end of the dry season (Sivakumar et al. 1993). Soils are generally very sandy and infertile, and are classified as arenosols throughout most of the study region (FAO 2007).

The five species included in this study (*C. glutinosum*, *C. micranthum*, *C. nigricans*, *G. senegalensis* [Combretaceae] and *P. reticulatum* [Caesalpiniaceae]) are widely used by rural communities in Niger and neighboring countries for construction poles, fuelwood, fodder, medicines, soil fertility improvement and soil/water conservation (Faye et al. 2011). They are commonly found in tropical dry forests (referred to below as woodlands) and in parkland agroforests. *Combretum glutinosum* and *C. nigricans* are short-statured trees (<12 m in height), while the other species are shrubs. *Combretum glutinosum* and *P.*

reticulatum are semi-evergreen, while the other species are deciduous during the dry season.

The five species were sampled roughly along latitudinal transects in four regions (Fig. 1) at the end of the dry season in 2011. We planned to sample 20 trees of each species per region, but we could not find trees of *C. nigricans* in regions 3 and 4, and only found 10 trees of *C. micranthum* in region 4. We maintained a minimum distance of 10 km between trees of the same species in order to ensure a broad geographic sampling. Trees were selected if they were produced by natural regeneration, and if the stem was not a coppice shoot, was undamaged, was growing relatively upright, and was within a predetermined diameter class (4–12 cm at 30 cm above ground level). We selected this diameter class because these stems are typically cut for construction poles and fuelwood so trees with larger stem diameters are relatively rare. It was not possible to sample trees of all five species at the same sample points due to differences in species' distribution and difficulty in finding trees that satisfied the selection criteria.

We recorded three qualitative site variables and geographical coordinates at the location of each sampled tree. Site variables included land use type (parkland agroforest or woodland), soil type (primarily sand or primarily rocks including laterite), and terrain type (flat, temporarily flooded or hill slope). Latitude, longitude and elevation were recorded with a GPS receiver, and used to obtain estimates of mean annual rainfall (mm) from the WorldClim database (www.worldclim.org). We have no information about the accuracy of the estimates for mean annual rainfall, but they may not be very accurate because there are

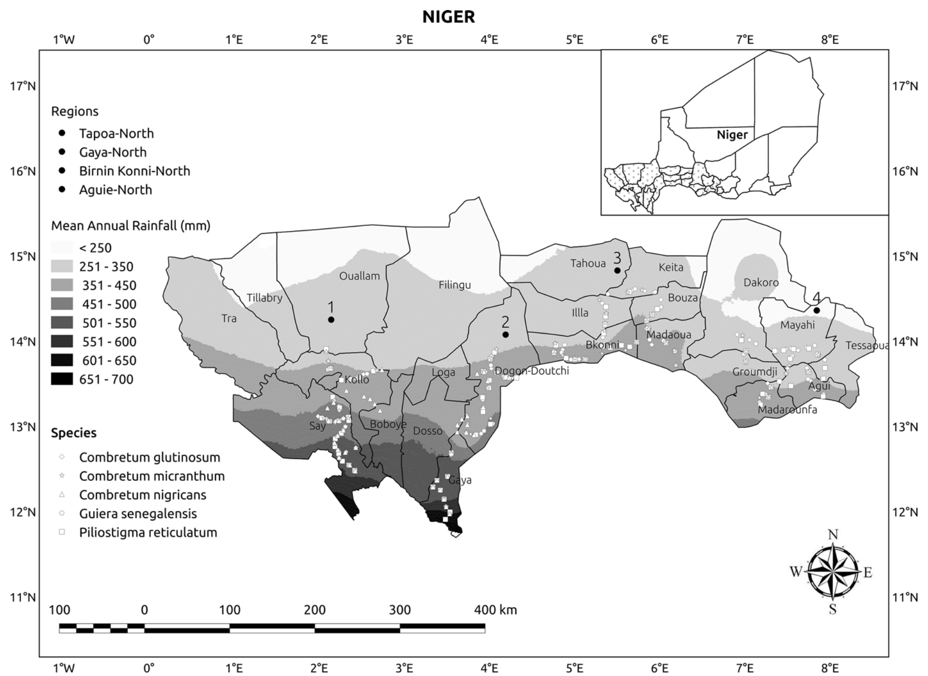

Fig. 1 Geographic location of five species sampled in four regions in southern Niger with mean annual rainfall isohyets across the sample regions, and map of Niger (*upper right*) with the location of the sample regions (*mottled area*)

few meteorological stations in Niger. The range in latitude, longitude and mean annual rainfall of sampled trees is shown in Fig. 1. Elevation ranged from 239 to 603 m.

Estimated mean annual rainfall at the location of the sampled trees decreased from south to north, west to east and from low to high elevation (Pearson r of mean annual rainfall with latitude, longitude and elevation, respectively = −0.920, −0.688 and −0.633; $P < 0.001$, N = 350). Elevation at the location of the sampled trees increased from south to north and from west to east (Pearson r of elevation with latitude and longitude = 0.646 and 0.794, respectively; $P < 0.001$, N = 350).

Sample size, mean elevation and mean annual rainfall by species, land use, soil and terrain types are given in "Appendix". *Guiera senegalensis* and *P. reticulatum* were sampled mainly in parkland agroforests, while *C. micranthum* and *C. nigricans* were sampled mainly in woodlands. Mean elevation was higher and mean annual rainfall was lower in parkland agroforests than in woodlands, i.e. parkland agroforests were more common in the north and east, while woodlands were more common in the south and west. The majority of trees were sampled on sandy rather than on rocky soils, and on flat terrain rather than on temporarily flooded sites and hill slopes. Trees were not sampled in all combinations of land use, soil and terrain types for all species.

Measurements of tree growth, wood density and carbon concentration

In the field, we measured height of each tree in cm with a telescopic measuring pole. The tree was then cut down, and a sample of the stem (30 cm long) was obtained between 30 and 60 cm above ground level. We labeled the north- and south-facing sides of the stem for reasons explained below.

In a laboratory, the bark was removed from each stem sample, and lines were drawn on the north and south-facing sides of the wood. Two disks, without nodes or defects, were cut from the lower part of the stem sample (31–34 cm above ground level). Disks were air-dried for one month to attain equilibrium moisture content prior to measurements.

One disk (2 cm thick) was used to measure stem diameter under bark and basic density. Diameter was measured in mm with a diameter tape at 31 cm above ground level. Basic density (oven-dry weight/green volume) was measured in kg m^{-3} using the water displacement method (ASTM 1997).

The other disk (1 cm thick) was used to determine the number and width of the annual rings at 33 cm above ground level. We measured the width of annual rings in the four cardinal directions in order to sample intra-ring variation. The lower surface of the disk was sanded so that the annual rings were clearly visible, and the four cardinal directions were labeled on the sanded surface. A digital image of the surface was produced, a digital grid was overlaid on the image, and the annual rings were marked on the image along the four cardinal directions. The number of rings was counted and used as an estimate of the tree's age. The width of each ring was measured in mm along each cardinal direction, and the mean width of each annual ring was calculated from the four values. The mean width of all the annual rings was then calculated (referred to below as mean ring width).

Sawdust was prepared from the remaining part of the air-dried stem samples (generally between 36 and 40 cm above ground level) and used to measure carbon concentration. Sawdust samples were oven-dried (70 °C) until they reached a constant weight. One subsample (0.5 g) per tree was analyzed using a carbon determinator (LECO C-144). This involved the complete combustion of the sample, measurement of CO_2 produced, and determination of carbon concentration in percent/ppm taking into account the sample weight, moisture content and calibration (calibrated with rice flour). At least part of the volatile carbon fraction was lost because the samples were oven dried, so the measured carbon concentration underestimates the total carbon concentration. The underestimate may be as much as 2.5% (Martin and Thomas 2011). The volatile carbon fraction is very labile. For the purpose of carbon sequestration by forests and harvested wood products, what really matters is the carbon that remains fixed for a long time, represented in this paper by the carbon concentration after oven drying.

Stem samples of some trees were damaged by wood-boring beetles, so we could not obtain all data from these trees. If we could not estimate age of a tree, then all data for that tree were excluded from the analyses.

Data analysis

The SAS statistical package (SAS Institute Inc. 2004) was used for all analyses, and the significance level was $\alpha \leq 0.05$ for all tests. The following procedures were used: Univariate to assess normality of residuals; Mixed (restricted maximum likelihood estimation method) for analysis of covariance and variance, Corr for Pearson correlations, and Reg for linear regressions. Data transformations were not considered necessary because the residuals from the analyses of variance and regressions exhibited normal distributions.

Values for height, stem diameter under bark, mean ring width, wood density and carbon concentration were adjusted for differences in tree age. We did an analysis of covariance for each variable of each species with only the covariate age in the model, and adjusted the data using the following formula: $Z_{i(jk)} = Y_{i(jk)} - \beta_{i(k)}(X_{j(k)} - X_k)$, where $Z_{i(jk)}$ = adjusted value of variable$_i$ of tree$_j$ of species$_k$, $Y_{i(jk)}$ = unadjusted value of variable$_i$ of tree$_j$ of species$_k$, $\beta_{i(k)}$ = effect of age on variable$_i$ of species$_k$, $X_{j(k)}$ = age of tree$_j$ of species$_k$, and X_k = mean age of species$_k$. Adjusted data were used for all analyses described below. Since data were adjusted separately for each species, trees with greater adjusted values for growth variables can be considered faster-growing trees within their particular species.

Analysis of variance was used to determine if growth variables, wood density and carbon concentration differed significantly among species and site variables. Regions were treated as blocks. The ANOVA model was: $Y_{ijklmn} = \mu + \alpha_i + \beta_j + \gamma_k + \delta_l + \eta_m + \theta_{ij} + \lambda_{ik} + \Omega_{il} + \psi_{im} + \varepsilon_{ijklmn}$, where Y_{ijklmn} = tree$_{\mathrm{n}}$ in treatment combination$_{\mathrm{ijklm}}$, μ = the grand mean, α_i = species$_{\mathrm{i}}$, β_j = block$_{\mathrm{j}}$, γ_k = soil type$_{\mathrm{k}}$, δ_l = land use type$_{\mathrm{l}}$, η_m = terrain type$_{\mathrm{m}}$, θ_{ij} = interaction between species$_{\mathrm{i}}$ and block$_{\mathrm{j}}$, λ_{ik} = interaction between species$_{\mathrm{i}}$ and soil type$_{\mathrm{k}}$, Ω_{il} = interaction between species$_{\mathrm{i}}$ and land use type$_{\mathrm{l}}$, ψ_{im} = interaction between species$_{\mathrm{i}}$ and terrain type$_{\mathrm{m}}$, and ε_{ijklmn} = residual error. Main effects (species, soil, land use, terrain), blocks and interactions were treated as fixed factors. Interactions between blocks and site variables were not tested because there were no observations for some site variables of some species in some blocks ("Appendix"). Least-squares means for main effects were compared using the Tukey HSD (honestly significant difference) test.

Based on previous research in Mali (Sotelo Montes et al. 2012), we expected that the effects of site variables on wood properties would differ among species. For this reason, we also did the ANOVA separately for each species. The ANOVA model was: $Y_{jklmn} = \mu + \beta_j + \gamma_k + \delta_l + \eta_m + \varepsilon_{jklmn}$, where Y_{jklmn} = tree$_{\mathrm{n}}$ in treatment combination$_{\mathrm{jklm}}$, μ = the grand mean, β_j = block$_{\mathrm{j}}$, γ_k = soil type$_{\mathrm{k}}$, δ_l = land use type$_{\mathrm{l}}$, η_m = terrain type$_{\mathrm{m}}$, and ε_{jklmn} = residual error.

Linear regression was used to investigate relationships between mean annual rainfall (independent variable) and growth variables, wood density and carbon concentration (dependent variables). Regressions were computed across species to determine if mean annual rainfall had a general effect on the dependent variables, and separately for each species to determine if the effect of rainfall on the dependent variables differed among species.

Pearson correlation coefficients were used to investigate linear relationships between growth variables and carbon concentration, between growth variables and wood density, and between wood density and carbon concentration of each species.

Results

Differences in growth, wood density and carbon concentration among species, land use, soil and terrain types

Data were adjusted for age by species, so differences in growth, wood density and/or carbon concentration between some species may reflect the difference in tree age. Mean age of sampled trees was 8.7, 9.2, 8.9, 8.0 and 7.5 years, respectively for *C. glutinosum*, *C. micranthum*, *C. nigricans*, *G. senegalensis* and *P. reticulatum*. Mean age was significantly greater for the three *Combretum* species compared with the other two species (Tukey HSD, $P < 0.001$).

Coefficients of variation were greater for growth variables than for wood density and especially carbon concentration in all five species (Table 1). This indicates that there was

Table 1 Differences in growth, wood density and carbon concentration among species in Niger

Variables[a]	P[b]	*C. glutinosum*	*C. micranthum*	*C. nigricans*	*G. senegalensis*	*P. reticulatum*
Mean[c]						
Height	**	3.23bc	3.02b	3.54c	3.02b	2.63a
Diameter	***	5.9b	5.2a	6.2c	5.4a	5.0a
Mring	***	0.33c	0.27a	0.32bc	0.32bc	0.30b
Density	***	695b	758c	756c	690b	581a
Carbon	***	41.2b	42.4c	40.6a	42.6c	40.9ab
Coefficient of variation (%)						
Height		19.3	23.7	20.0	17.5	20.2
Diameter		15.7	13.3	19.2	15.5	19.0
Mring		17.7	15.4	16.9	17.2	19.2
Density		6.0	5.8	5.5	5.9	4.4
Carbon		1.1	1.5	3.1	1.4	1.1

[a] Variables: Height = tree height (m), Diameter = stem diameter (cm) under bark measured at 32 cm above ground level, Mring = mean width (cm) of annual rings measured at 33–34 cm above ground level, Density = basic wood density (kg m^{-3}) measured at 31–33 cm above ground level, Carbon = carbon concentration (%) of wood measured at 36–40 cm above ground level; values adjusted for tree age

[b] P = probability of F for testing effect of species: *** $P \leq 0.001$; ** $P \leq 0.01$

[c] Tabled means are least squares means: means with the same letter are not significantly different ($P > 0.05$) and those with different letters are significantly different ($P \leq 0.05$) based on Tukey HSD test; sample size = 75 for *C. glutinosum*, 70 for *C. micranthum*, 40 for *C. nigricans*, 79–80 for *G. senegalensis*, 77–79 for *P. reticulatum*

relatively little intra-specific variation in wood density and especially in carbon concentration, compared with growth variables.

Tree growth, wood density and carbon concentration differed significantly among species (Table 1). Tree height, stem diameter and mean ring width were generally greater for the tree species (*C. glutinosum* and *C. nigricans*) than for the shrub species. Wood density was greatest for *C. micranthum* and *C. nigricans* and lowest for *P. reticulatum*. Carbon concentration was greatest for *C. micranthum* and *G. senegalensis* but lowest for *C. nigricans* (in contrast to density).

Two interactions between species and site variables were significant for carbon concentration: species by soil type ($P < 0.05$, DF = 4/304) and species by terrain type ($P < 0.01$, DF = 7/304). This indicates that the effects of soil and terrain types on carbon concentration were not the same for all species. Interactions between species and site variables were not significant for growth variables and wood density ($P > 0.05$).

Table 2 Differences in growth, wood density and carbon concentration of species between land use and terrain types in Niger

Species[a]	Variables[b]	P[c]	Mean (standard error of mean in parentheses)[d]		
			Land use type		
			Parkland	Woodland	
All species	Diameter	***	5.7b (0.1)	5.3a (0.1)	
	Mring	*	0.32b (0.01)	0.30a (0.01)	
C. glutinosum	Diameter	*	6.4b (0.3)	5.8a (0.2)	
G. senegalensis	Density	*	682a (8)	708b (10)	
			Terrain type		
			Temporarily flooded	Flat	Hill slope
All species[e]	Carbon	*	41.6a (0.2)	41.5a (0.1)	41.5a (0.1)
C. nigricans	Carbon	*	–	40.4a (0.2)	42.0b (0.7)

[a] Results shown only for variables with significant difference between land use or terrain types

[b] Variables: Diameter = stem diameter (cm) under bark measured at 32 cm above ground level, Mring = mean width (cm) of annual rings measured at 33–34 cm above ground level, Density = basic wood density (kg m^{-3}) measured at 31–33 cm above ground level, Carbon = carbon concentration (%) of wood measured at 36–40 cm above ground level; values adjusted for tree age

[c] P = probability of F for testing effect of land use and terrain types: *** $P \leq 0.001$; * $P \leq 0.05$

[d] Tabled means are least squares means: means with the same letter are not significantly different ($P > 0.05$) and those with different letters are significantly different ($P \leq 0.05$) based on Tukey HSD test; *C. nigricans* found on only two of the three terrain types; sample size = 341–344 for all species, 75 for *C. glutinosum*, 40 for *C. nigricans*, 79–80 for *G. senegalensis*

[e] Significant difference based on F ratio, but not significant based on Tukey HSD test

In the analysis across species, land use type had a significant effect on stem diameter and mean ring width (Table 2). Mean values for these variables were greater in parkland agroforests than in woodlands.

In the analysis across species, terrain type had a significant effect on carbon concentration (Table 2). Carbon concentration was slightly higher on temporarily flooded sites than on flat terrain and hill slopes, but the differences were not significant based on the Tukey HSD test.

Analyses within species showed that land use type had a significant effect on stem diameter of *C. glutinosum*, and wood density of *G. senegalensis* (Table 2). Stem diameter of *C. glutinosum* was greater in parkland agroforests than in woodlands, while wood density of *G. senegalensis* was greater in woodlands than in parkland agroforests.

Terrain type had a significant effect only in *C. nigricans* (Table 2). Carbon concentration was greater on hill slopes than on flat terrain.

Differences in growth, wood density and carbon concentration related to mean annual rainfall

Only seven of the 30 regressions with mean annual rainfall were significant, and most of them explained less than 15% of the variation (Table 3). Tree height across species and in *C. micranthum*, *G. senegalensis* and *P. reticulatum* increased with mean annual rainfall. Carbon concentration increased with mean annual rainfall in *C. nigricans*, but decreased with mean annual rainfall in *P. reticulatum*. Wood density decreased with mean annual rainfall in *C. micranthum*.

Correlations between growth, wood density and carbon concentration

Correlations between growth and carbon concentration were similar for the three *Combretum* species and *P. reticulatum* (Table 4). Trees of these species with greater values for

Table 3 Linear regression equations of tree height, wood density and carbon concentration with mean annual rainfall in Niger

Species[a]	Dependent variables[b]	Intercept[c]	Rainfall[c]	r^2 and P[c]
All species	Height	1.820	3.040×10^{-3}	0.128***
C. micranthum	Height	0.882	5.340×10^{-3}	0.335***
	Density	852	-2.268×10^{-1}	0.168***
C. nigricans	Carbon	37.215	7.020×10^{-3}	0.134*
G. senegalensis	Height	1.984	2.630×10^{-3}	0.152***
P. reticulatum	Height	1.948	1.730×10^{-3}	0.069*
	Carbon	41.484	-1.520×10^{-3}	0.071*

[a] Only the statistically significant regressions are shown

[b] Dependent variables: Height = tree height (m), Density = basic wood density (kg m^{-3}) measured at 31–33 cm above ground level, Carbon = carbon concentration (%) of wood measured at 36–40 cm above ground level; values adjusted for tree age

[c] Intercept = equation intercept; Rainfall = regression coefficient for mean annual rainfall (mm); r^2 = coefficient of determination; P = probability of F for testing effect of mean annual rainfall (*** $P \leq 0.001$, * $P \leq 0.05$); sample size = 344 for all species, 70 for *C. micranthum*, 40 for *C. nigricans*, 80 for *G. senegalensis*, 77–79 for *P. reticulatum*

height, stem diameter and/or mean ring width (referred to below as larger, faster-growing trees) tended to have greater carbon concentration. Correlations were generally stronger with height and/or stem diameter than with mean ring width.

Correlations between growth and wood density differed in sign between *C. micranthum* and *G. senegalensis* (Table 4). Larger, faster-growing trees tended to have lower wood density in *C. micranthum* but higher wood density in *G. senegalensis*.

Correlations between wood density and carbon concentration were generally not significant (Table 4). Trees with greater wood density tended to have higher carbon concentration only in *G. senegalensis*.

Discussion

Differences in growth, wood density and carbon concentration among species

Mean values for wood density of the five species were similar to those reported in other studies in natural populations in the Sahelian and Sudanian ecozones of West Africa. For example, basic density was 694, 760, 755, 658 and 647 kg m^{-3}, respectively for *C. glutinosum*, *C. micranthum*, *C. nigricans*, *G. senegalensis* and *P. reticulatum* sampled in Burkina Faso (Nygård and Elving 2000), and 666, 673 and 530 kg m^{-3}, respectively for *C. glutinosum*, *G. senegalensis* and *P. reticulatum* sampled in Mali (Sotelo Montes et al. 2012).

Wood carbon concentration has not been studied in dry tropical forests of Africa. Mean wood carbon concentration of the five species in this study was 41.5%, which is 5.6% lower than the mean of 134 angiosperm tree species sampled in humid tropical forests in Bolivia, Costa Rica, Panama, the Philippines and Uganda (Thomas and Martin 2012). Other researchers have reported a positive correlation between tree size and wood carbon concentration (Elias and Potvin 2003; Thomas and Malczewski 2007; Castaño-Santamaria and Bravo 2012). The lower mean wood carbon concentration of the species in this study may be due to their smaller stature, compared with tree species in humid tropical forests.

Table 4 Pearson correlation coefficients between growth, wood density and carbon concentration of species in Niger

Species[a]	Variables[b]	Height[b]	Diameter[b]	Mring[b]	Density[b]
C. glutinosum	Carbon	0.274*[c]	0.399***	0.317**	NS
C. micranthum	Carbon	NS	0.268*	NS	NS
	Density	−0.290*	NS	NS	–
C. nigricans	Carbon	0.332*	NS	NS	NS
G. senegalensis	Carbon	NS	NS	NS	0.283*
	Density	0.279*	0.321**	0.328**	–
P. reticulatum	Carbon	NS	0.240*	NS	NS

[a] Only the statistically significant correlations are shown

[b] Variables: Height = tree height, Diameter = stem diameter under bark measured at 32 cm above ground level, Mring = mean width of annual rings measured at 33–34 cm above ground level, density = basic wood density measured at 31–33 cm above ground level, Carbon = carbon concentration of wood measured at 36–40 cm above ground level; values adjusted for tree age

[c] Significance of Pearson r: *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, NS $P > 0.05$; sample size = 75 for *C. glutinosum*, 70 for *C. micranthum*, 40 for *C. nigricans*, 79–80 for *G. senegalensis*, 77 for *P. reticulatum*

There was no consistent relationship between mean wood density and carbon concentration of the species in this study. Others have also reported that species with higher carbon concentration do not necessarily have denser wood (Zhang et al. 2009). This may reflect inter-specific differences in the concentrations of cellulose, lignin and non-structural carbohydrates (Martin and Thomas 2011), and vessel wall thickness and lumen diameter (Hoeber et al. 2014). Wood with thicker vessel walls and narrower vessel lumen tends to be denser, but the ratio of cellulose to lignin in the vessel walls affects carbon concentration and wood density because lignin contains more carbon than cellulose. In addition, an increase in the amount of non-structural carbohydrates can decrease carbon concentration in the wood (Poorter and Kitajima 2007).

Coefficients of variation indicated that there was relatively little intra-specific variation in wood density and especially in carbon concentration compared with growth variables. This is consistent with other studies of wood density in the Sahelian and Sudanian ecozones of West Africa (Nygård and Elving 2000; Sotelo Montes and Weber 2009; Weber and Sotelo Montes 2010; Sotelo Montes et al. 2012), and studies of carbon concentration in other regions (Francis 2000; Watzlawick et al. 2014). Results suggest that variation in the amount of carbon in the stem is determined primarily by tree height and stem diameter, rather than by wood density and carbon concentration.

Mean age of the trees differed among some species, but the largest difference was only 1.7 years. Based on previous research, these small differences in tree age would have little if any effect on inter-specific differences in wood properties (Lemenih and Bekele 2004; Kumar et al. 2010; Sotelo Montes et al. 2012).

Species were sampled at relatively young ages in this study (mean age <10 years). Mean values for growth variables and probably also for wood density and carbon concentration would have been greater if we had also sampled older trees. Future studies should attempt to sample trees from the entire age distribution of the species.

Differences in growth, wood density and carbon concentration due to land use type, soil type, terrain type and mean annual rainfall

Mean stem diameter and ring width across species were greater in parkland agroforests than in woodlands. This may reflect higher soil fertility and/or lower tree density in parkland agroforests compared with woodlands, but we did not quantify these variables. Farmers increase soil fertility in parkland agroforests by burning brush, which increases soil calcium and potassium contents (Ragland et al. 1991), and by adding manure. Parkland agroforests contain fewer trees/shrubs per hectare than woodlands (Boffa 1999), and stem diameter is generally greater in lower-density stands (Jiang et al. 2007).

Most effects of land use, soil and terrain types on growth, wood density and carbon concentration were not significant in this study. In Mali, the effects of land use, soil and terrain types were significant for growth variables in some species (Sotelo Montes et al. 2017a) but not for wood density (Sotelo Montes et al. 2012). The site variables used in this study and in Mali were qualitative. In addition, sample sizes for the species differed among the land use, soil and especially terrain types, reflecting differences in species' distributions. Future research should quantify environmental differences within the land use, soil and terrain types (e.g., number of trees per hectare, soil texture, rockiness, soil fertility, depth to the water table, percent slope, land use history) and, if possible, sample similar numbers of trees in each land use, soil and terrain type.

Mean height across species increased from the drier to the more humid sample locations, as one would expect (Shackleton and Scholes 2011). Analysis within species indicated that the relationship with rainfall was significant in the shrub species, but not in the tree species. This may reflect differences in rooting depth between the shrub and tree species (assuming that trees have deeper roots) and the depth of the water table, but we did not quantify these variables. If species differ in rooting depth and the depth of the water table varies spatially or temporally, then the relationship between mean annual rainfall and growth may not be significant for deeper-rooting species because they may be able to extract soil water during the dry season (Gourlay 1995).

Effects of mean annual rainfall on wood density and carbon concentration differed among some species in this study. Wood density was greater in drier locations in one species, but it did not vary significantly with mean annual rainfall in four species. The relationship between mean annual rainfall and wood density was also not significant for *C. glutinosum*, *G. senegalensis* and *P. reticulatum* in Mali (Sotelo Montes et al. 2014). Carbon concentration varied with mean annual rainfall in two species, but the relationships were in contrasting directions. Differences like these are expected in studies of variation in wood properties in natural populations (Sotelo Montes et al. 2013, 2014, 2017a, b). As others have noted, any environmental factor that affects tree growth may also affect wood properties and correlations between growth and wood properties, and different species and trees within species respond differently to environmental factors (Zobel and van Buijtenen 1989).

Correlations between growth, wood density and carbon concentration

Wood density was positively correlated with carbon concentration in one species, but the correlation was not significant in four species. Results indicate that wood density is not necessarily a useful proxy variable for carbon concentration, as some have suggested (Elias and Potvin 2003). Others have also reported that the correlation between wood density and carbon concentration is not significant in some species (Navarro et al. 2013).

The correlation between growth and wood density was positive, negative or not significant in the five species. Other studies have reported that the correlation between growth and wood density is either positive or not significant in tree/shrub species in the Sahelian and Sudanian ecozones of Mali and Niger (Sotelo Montes and Weber 2009; Weber and Sotelo Montes 2010; Sotelo Montes et al. 2014). Further research is needed to understand why the correlation differs in sign among some species.

The correlation between growth and carbon concentration was positive in four species. This is consistent with studies of other species (Elias and Potvin 2003; Thomas and Malczewski 2007; Castaño-Santamaria and Bravo 2012). The result means that carbon concentration in the four species tended to be greater in larger, faster-growing trees which tended to be located in parkland agroforests (rather than woodlands) and in more humid locations.

Assessment of species for carbon sequestration in parkland agroforests

In this section we assess which species in this study would be better for carbon sequestration in parkland agroforests in southern Niger. The assessment is based on height growth rate (i.e., mean height divided by mean age), carbon content per cubic meter of wood (i.e., product of mean basic density and mean carbon concentration), correlations between height, wood density and carbon concentration, and farmers' preferences for the species.

Species that grow faster and have greater carbon content per cubic meter of wood would be preferred for carbon sequestration. Height growth rate was 37, 33, 40, 38 and

35 cm year^{-1}, respectively for *C. glutinosum*, *C. micranthum*, *C. nigricans*, *G. senegalensis* and *P. reticulatum*: based on this criterion, the best three species were *C. nigricans*, *G. senegalensis* and *C. glutinosum*. Carbon content per cubic meter of wood was 286, 321, 307, 294 and 238 kg m^{-3}, respectively for *C. glutinosum*, *C. micranthum*, *C. nigricans*, *G. senegalensis* and *P. reticulatum*: based on this criterion, the best three species were *C. micranthum*, *C. nigricans* and *G. senegalensis*.

Species that have positive correlations between height, wood density and carbon concentration would also be preferred for carbon sequestration. *Guiera senegalensis* was the only species that had positive correlations between height and wood density and between wood density and carbon concentration. *Combretum micranthum* had a negative correlation between height and wood density. Height and carbon concentration were positively correlated in *C. glutinosum* and *C. nigrican*s. Based on these correlations, the best three species were *C. glutinosum*, *C. nigricans* and *G. senegalensis*.

In surveys in southern Niger, farmers ranked their 55 preferred species based on their functional utility in parkland agroforests (Faye et al. 2011: functions included human food, medicines, animal food, wood/energy/fiber, soil fertility improvement, soil/water conservation and shade). *Guiera senegalensis* and *P. reticulatum* were equally ranked #3 while the three *Combretum* species received lower rankings (not among the top 10 species).

Based on this assessment, *G. senegalensis* would be the best of the five species to promote for carbon sequestration in parkland agroforests in southern Niger. Although its growth rate and carbon content per cubic meter of wood were lower than some of the other species, farmers considered *G. senegalensis* very useful for their parkland agroforests. Among the other species, *C. glutinosum* and *C. nigricans* would be better than *C. micranthum* and *P. reticulatum* for carbon sequestration based on their growth rate, carbon content per cubic meter of wood and/or correlations.

Conclusions and recommendations

Mean annual rainfall and land use, soil and terrain types did not have strong effects on growth, wood density and carbon concentration of the five species, and some effects differed among species. Mean height across species increased with mean annual rainfall. Mean stem diameter and ring width across species were greater in parkland agroforests than in woodlands. Results suggest that the carbon content in the stem across species increases with mean annual rainfall and is greater in parkland agroforests than in woodlands, but research is needed to quantify these differences.

Carbon concentration tended to be higher in larger, faster-growing trees of four species. Carbon concentration was not correlated with wood density in most species. Correlations between wood density and growth differed in sign among some species.

Based on this research, we recommend promoting management of natural regeneration and small-scale plantations of *C. glutinosum*, *C. nigricans* and *G. senegalensis* for carbon sequestration in parkland agroforests in southern Niger, especially in zones with higher mean annual rainfall. Preference surveys suggest, however, that farmers may be more likely to increase the abundance of *P. reticulatum* than the abundance of *C. glutinosum* and *C. nigricans* in their parkland agroforests. We also recommend research on variation in growth, wood density and carbon concentration of other native tree and shrub species that farmers manage in tropical dry forests and parkland agroforests in West Africa and other regions in Africa.

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Appendix

See Table 5.

Table 5 Sample size (N), mean elevation (E, m) and mean annual rainfall (R, mm) by species, land use, soil and terrain types in Niger

Sample group	Variable	*C. glutinosum*	*C. micranthum*	*C. nigricans*	*G. senegalensis*	*P. reticulatum*
All trees	N	75	70	40	80	79
	E	310	292	239	306	303
	R	401	410	464	399	403
Parkland agroforests	N	39	20	6	50	50
	E	365	351	241	327	335
	R	347	345	449	365	372
Sandy soil	N	34	14	6	45	42
	E	351	337	241	318	316
	R	349	349	449	368	377
Temporarily flooded	N	–[a]	2	–	–	–
	E	–	219	–	–	–
	R	–	420	–	–	–
Flat	N	28	11	6	40	39
	E	348	352	241	319	315
	R	350	338	449	372	373
Hill slope	N	6	1	–	5	3
	E	365	410	–	311	323
	R	344	326	–	338	421
Rocky soil	N	5	6	–	5	8
	E	455	381	–	407	433
	R	340	334	–	336	348
Temporarily flooded	N	–	1	–	–	–
	E	–	380	–	–	–
	R	–	354	–	–	–
Flat	N	4	4	–	2	5
	E	448	365	–	348	420
	R	341	329	–	316	347
Hill slope	N	1	1	–	3	3
	E	483	447	–	446	454
	R	339	335	–	350	350
Woodlands	N	36	50	34	30	29
	E	261	269	239	270	253
	R	457	437	467	456	454

Table 5 continued

Sample group	Variable	*C. glutinosum*	*C. micranthum*	*C. nigricans*	*G. senegalensis*	*P. reticulatum*
Sandy soil	N	17	27	12	19	16
	E	240	273	233	275	241
	R	447	433	482	454	466
Temporarily flooded	N	2	4	–	5	5
	E	255	396	–	263	252
	R	365	379	–	443	489
Flat	N	14	22	12	13	10
	E	238	246	233	284	236
	R	465	446	482	453	462
Hill slope	N	1	1	–	1	1
	E	239	395	–	213	233
	R	353	373	–	524	401
Rocky soil	N	19	23	22	11	13
	E	279	264	242	263	267
	R	466	441	459	458	439
Temporarily flooded	N	2	–	–	–	–
	E	230	–	–	–	–
	R	477	–	–	–	–
Flat	N	13	16	19	8	11
	E	255	263	244	240	254
	R	495	440	453	452	451
Hill slope	N	4	7	3	3	2
	E	382	265	226	323	337
	R	366	443	496	476	377

[a] – No trees were sampled in this combination of land use, soil and terrain types

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